Water availability as driver of birch mortality in Hustai National Park, Mongolia

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A B S T R A C T

Trees in the forest-steppe ecotones face stress due to reduced water availability as a consequence of more extreme seasonal fluctuations in precipitation and temperature. Together with browsing pressure this can hinder tree growth, tree regeneration and competition between trees and grasses. We studied the impact of both stress factors on the mortality of birch trees in two forest sites at Hustai National Park, Mongolia, by applying tree-ring research to determine growth-limiting factors and assessing browsing pressure on young and adult birch. We expected warm and dry summer conditions as main growth limiting factor. Moreover, we expected a positive relation between deer density and tree mortality with browsing mainly affecting smaller trees with a low diameter at breast height (DBH). We found that the growth in both birch populations is mainly driven by winter precipitation and – to a lesser extent – negatively affected by high summer temperature. This suggests that water availability as defined by soil moisture, especially at the beginning of the growing season is crucial for birch growth in our study area. For mortality we found significant differences between both populations, but no significant relationship with deer density. In plots with high mortality rates mean tree height of the remaining living trees decreased. These results suggest that under expected climate change with declining annual precipitation rates, the birch forest of Hustai National Park is converting into a steppe ecosystem, like described for other forest ecosystems in this ecotone.

1. Introduction

To better understand forest-cover dynamics in the forest-steppe ecotone and predict future shifts in this complex ecosystem, more knowledge is required on the role of specific climatic and biotic factors affecting tree mortality and tree growth. Trees in the forest-steppe ecotones face considerable stress due to more extreme seasonal fluctuations in precipitation and temperature as a consequence of climate change, which reduces their growth and competitive ability (Dulamsuren et al., 2014). An increase in the frequency of drought events (*i.e.* increasing temperature and reduced mean annual precipitation; Allen et al., 2010) tends to reduce tree vigour (Anderegg et al., 2015; Choat et al., 2008; Suarez et al., 2004) and moreover affects tree regeneration (Will et al., 2013). Conversely, above-average precipitation during the growing season (Block and Treter, 2013), wet and cool summers (Dulamsuren et al., 2010) and wet conditions during the previous year and spring (Dulamsuren et al., 2014), positively influence tree growth of larch in Northern Mongolia. Recently, Gradel et al. (2017) found that current growth of birch in Northern Mongolia

was favoured by wet conditions during the previous year and winter, whereas above-average temperature negatively affected birch growth.

Browsing pressure by ungulates might benefit tree species that are less sensitive to herbivory (Kirby, 2001; Seager et al., 2013; Tanentzap et al., 2011) and can moreover enhance the competitive disadvantage of trees relative to grasses in the forest-steppe ecotone (Wallis de Vries et al., 1996). However, besides browsing, red deer also damage trees by bark stripping, which results in reduced tree growth and increased vulnerability to fungal infestation and storm damage, and hence risk of mortality (Akashi and Nakashizuka, 1999; Månsson and Jarnemo, 2012). Both lead to major shifts in species richness, vegetation structure and the composition of understory and canopy vegetation (Seager et al., 2013).

Our study area, Hustai National Park, is located in the Siberian taiga of Mongolia. From 1994 to 2000, mountain steppe has replaced 12% of the forest area (Bayarsaikhan et al., 2009), and this trend has continued since. In the National Park, a complex balance exists between forest cover and the presence of red deer (*Cervus elaphus*), predating wolf (*Canis lupus*), Przewalski horse (*Equus ferus przewalskii*) and livestock. A
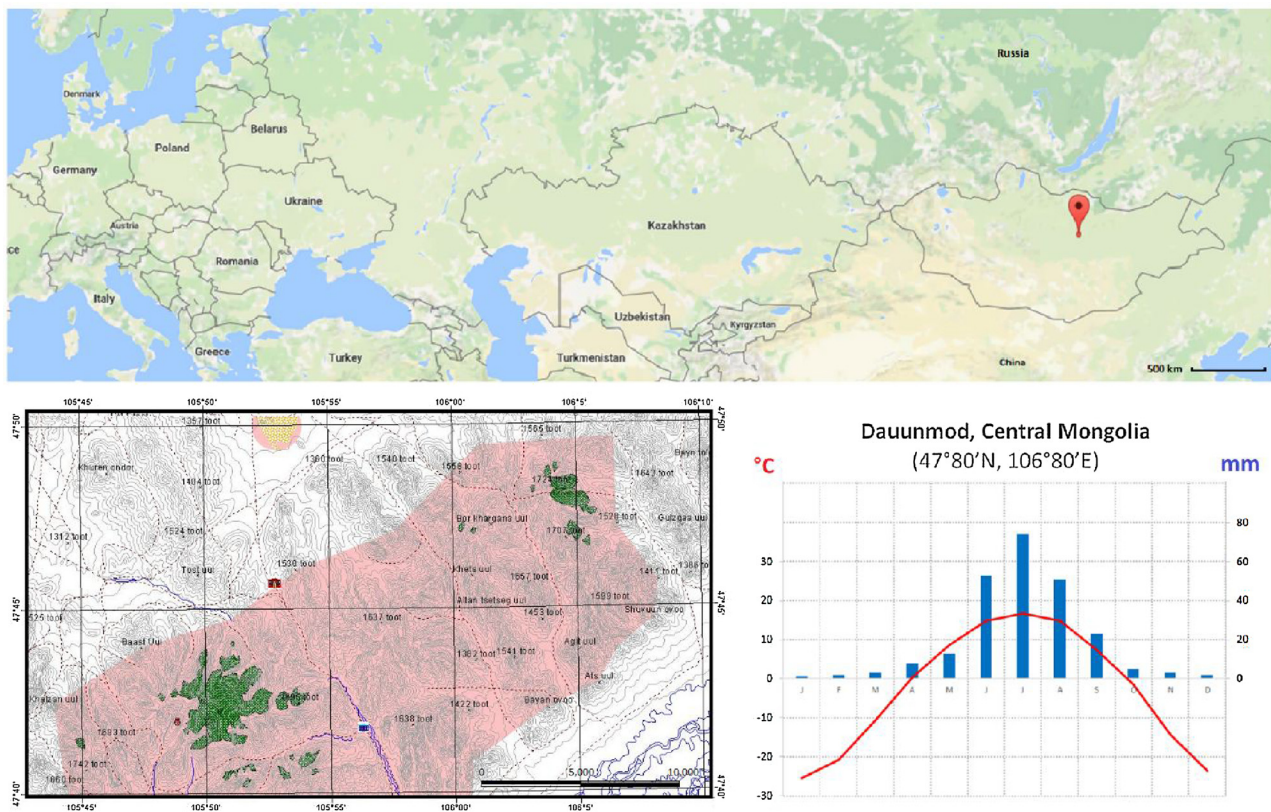

Fig. 1. (a) Location of Hustai National Park (red balloon; source: Google Maps); (b) location of the study areas within the National park (green areas; source: Hustai National Park); (c) climate diagram with monthly average temperature (°C, red line) and precipitation (mm, blue bars) for the period 1937–1990 (source: http://climexp.knmi.nl) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

decline in forest cover can have cascading effects in the forest-steppe ecotone (Anenkhonov et al., 2015): a further reduction in forest cover, *e.g.* through failing tree regeneration under higher soil temperatures and increased evapotranspiration during summer (Will et al., 2013), likely reduces the number of red deer, as forests act as browse resource and hiding spots from wolves. Reduction of deer as the main food source of wolves (Jędrzejewski et al., 2000, 2002; van Duyne et al., 2009) can trigger a shift in wolf diet from red deer to Przewalski horse. Forest cover is thus a key factor to predict whether the precious Przewalski horse can prevail in Hustai National Park.

The forest of Hustai National Park consists of two areas (West and East forest) dominated by birch (*Betula platyphylla*), growing on the northern and eastern facing slopes, where the permafrost layer is closest to the soil surface (Wallis de Vries et al., 1996); on the other slopes mountain steppe dominates (Bayarsaikhan et al., 2009). Both forests show tree mortality, but visual observations suggest a higher mortality in the West forest, possibly related to a higher deer density. To assess tree mortality in Hustai National Park and the reasons behind it, we investigated site conditions (rock cover, elevation and exposure), browsing pressure (deer density) and tree characteristics (tree density, tree height, DBH distribution, mortality rate) in both forest areas.

Tree-ring research was applied to estimate tree age (*e.g.* Tolera et al., 2013; Vlam et al., 2014) and radial growth dynamics in both birch populations. We tested the prediction that precipitation during the growing season is the main driver of birch growth in both forest areas. High summer temperature is assumed to negatively influence tree growth as high evaporation rates may lead to water shortage and early growth stop. Browsing pressure expressed by higher deer density is expected to increase mortality of especially young, small-diameter birches.

2. Methods

2.1. Study site

Fieldwork was conducted in Hustai National Park (47°50′N and 106°00′E), Töv Province, Mongolia. Hustai National Park covers in total 49,900 ha (Wit and Bouman, 2006). The West forest covers an area of c. 1700 ha on the North- and East-facing slopes at about 1700 m, whereas the East forest covers an area of c. 300 ha on the East-facing slopes at about 1600 m (Fig. 1b). These two birch forests are located more than 20 km apart from each other. The climate is continental, with average temperature ranging from −20 °C in January to 20 °C in July, with an annual precipitation of 220 mm (1993–2004; Sietses et al., 2009). About 70% of the rain falls between April and September (Fig. 1c; Wallis de Vries et al., 1996).

2.2. Fieldwork

During the period from May to July 2015, in total 44 plots of 10 × 10 m were randomly established in the East (12) and West forest (32) to assess tree characteristics, tree mortality and site-related aspects. In order to measure tree characteristics homogenous in both forests, the number of plots was based on the size of the two areas. Individual plots were established at least 100 m apart from each other. Within each plot all living and dead trees higher than 200 cm were detected and diameter at breast height (DBH in cm) and tree height (cm) was measured. From the share of dead and living trees recent birch mortality was calculated (%) per plot. Regeneration strategy was indicated in each plot for trees smaller than 200 cm and was defined as natural regeneration from seeds or regeneration from root systems of adult trees. In each plot the number of dung pellet groups was registered to estimate the relative abundance of deer. The percentage of

recently stripped bark by red deer was recorded for all trees taller than 200 cm.

Elevation was recorded to indicate the depth of the permafrost layer, since permafrost is closer to the soil surface at higher elevation and contributes to soil moisture content during summer thaw (Wallis de Vries et al., 1996). Additionally, rock cover (%) was visually approximated, since rock cover is also expected to improve soil conditions with respect to soil moisture content by improving rainfall infiltration and reducing direct radiation on the soil surface and evaporation (Pariente, 2000).

For tree-ring research, two increment cores each were extracted at c. 1 m stem height from in total 30 randomly selected birch trees (> 10 cm DBH). Twenty trees were located in the larger West forest and 10 trees were located in the East forest. At the lab the increment cores were glued in wooden holders, cut with a Stanley knife and treated with chalk to detect the ring boundaries (Gärtner et al. 2015).

2.3. Data analysis

Birch mortality per plot (%) and mean DBH per plot (cm) were compared between the West and East forest using a Mann Whitney U test to examine if birch mortality and the distribution of DBH classes differed. Deer density (number of dung pellet groups per plot) was compared between the two areas using an independent t-test. A Generalized Linear Model (GLM) was used to examine the correlation between tree mortality and respectively browsing indicators (number of dung pellet groups, bark stripping) and site conditions (rock cover, elevation) as well as tree characteristics (tree height, DBH), using a backward elimination of variables that were not significant.

Tree-ring width was measured using a LINTAB measuring table (1/100 mm accuracy) and TSAP-Win software (Rinn, 2003). Ring-width series were visually and statistically cross-dated within and between trees (program COFECHA: Grissino-Mayer, 2001; Holmes, 1983). Trends were eliminated by fitting a negative exponential curve or linear regression curve (program ARSTAN: Cook and Peters, 1981). The resulting index series were averaged into two site chronologies (West & East) and one regional ring-width chronology calculated from all 49 cross-dated series of 25 birches from both sites. Statistical characteristics of the ring-width series, *i.e.* mean ring width, standard deviation (SD), autocorrelation (AC), and mean sensitivity (MS) are compared between sites to evaluate differences in growth rate and variation patterns (*e.g.* Weemstra et al., 2013).

Multiple regression analyses were used to compare the variation in the ring-width chronologies over the last 75 years with variation in monthly average temperature and the monthly sum of precipitation. Precipitation records covering the period from 1937 to 1990 and temperature data from 1937 to 2014 was obtained from a weather station at Dauunmod, Central Mongolia (47°80′N, 106°80′E; KNMI Climate Explorer, http://climexp.knmi.nl; Fig. 1c), located at a distance of 70 km from Hustai National Park. Precipitation records from 1999 to 2014 were obtained from the weather station at Hustai National Park (47°50′N, 106°00′E); precipitation records from 1991 to 1998 are lacking.

3. Results

3.1. Tree mortality

In total we recorded 51 living and 134 dead birch trees in the West forest (159 living trees/ha) and 109 living and 28 dead birch trees in the East forest (908 living trees/ha) (Table 1). Birch mortality (%) was significantly higher (Mann Whitney U test: U = 47; p < 0.001) in the West than in the East forest. In the West forest, 40% of the plots had a

Table 1
Overview of the forest characteristics elevation (m), average rock cover (%), average number of dung pellet groups, average bark stripping (%), total tree density, mean tree height and mean DBH of living and dead birch trees, and average tree mortality (%) in investigated plots (n) of the two forest areas.

	West forest (n = 32)	East forest (n = 12)
Elevation (m)	1644–1824	1591–1648
Rock cover (%)	14	0
Dung pellet groups (n/plot)	14	9
Bark stripping (%)	8	3
Tree density living birch (trees/ha)	159	908
DBH living birch (cm)	14	13
Tree height living birch (cm)	503	695
Tree density dead birch (total n)	134	28
DBH dead birch (cm)	14	14
Tree height dead birch (cm)	596	778
Tree mortality (%)	69	21
Regeneration from roots (n)	122	68
Regeneration from seeds (n)	3	22

mortality rate of 100%. The DBH of living trees ranged from 2 to 24 cm in the West forest and from 1 to 33 cm in the East forest, with no difference in average DBH between plots in the two areas (Mann Whitney U test: U = 99.5; p > 0.05).

Tree regeneration from seeds was limited in the forests of Hustai National Park, with only 2% in the West forest (3 out of 125 trees smaller than 200 cm) and 24% in the East forest (22 out of 90 trees; Table 1 & Fig. 2). This means that regeneration in Hustai National Park mainly occurs from the root systems of adult trees. The number of dung pellet groups ranged from 5 to 28 pellets in plots of the West forest and from 0 to 17 pellets in those of the East forest (independent t-test: F = 0.845; p < 0.05) indicating that deer density was generally higher in the West forest than in the East forest.

At plot level, mean tree height of the remaining living trees decreased with increasing birch mortality (GLM, $F_{4,94} = -8.931$, p < 0.01), whereas mean DBH increased (GLM, $F_{4,94} = 7.722$, p < 0.05; Fig. 3), most likely due to the absence of young, small-diameter trees. This indicates that on average fewer tall and small-diameter living trees were present in plots with increasing mortality rates (> 50%), whereas no such correlation was found in plots with mortality rates of < 50% and 100% (Fig. 3). No significant correlation was found between birch mortality and mean DBH of dead trees, deer density, bark stripping, rock cover and elevation.

3.2. Tree-growth patterns

Growth rates and tree-ring patterns were very similar between the birch populations in the West (mean sensitivity = 0.51; first order autocorrelation = 0.57) and East forest (MS = 0.48; AC1 = 0.55). This is also reflected in the growth trajectories of the individual birch trees from both areas (Fig. 4). Although growth rate (slope) between individual trees in the two areas varied, individual trees cross-dated very well within both areas, but also between the two areas (Fig. 5a), indicating a high degree of common variation across time. The EPS values for both data collectives were well above 0.85 (Wigley et al., 1984) throughout the entire study period, which suggests that the chronologies are reliable for analysing climate-growth relationships.

3.3. Tree growth and climate

The climate-growth analyses revealed that the birches of both areas similarly and strongly positively respond to winter precipitation (linear regression, West forest: $F_{1,68} = 10.80$, p < 0.01; and East forest:
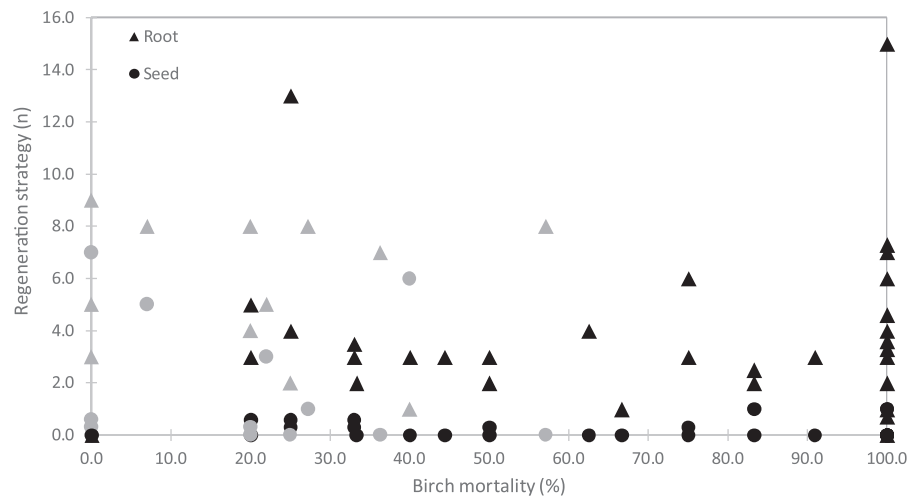
Fig. 2. Relationship between average birch mortality (%) and number of regenerated, small trees (< 200 cm) from seeds (dots) and from the root systems of adult trees (triangles) in either the West forest (black; n = 32) or East forest (grey; n = 12).

$F_{1,68} = 13.48$, p < 0.001). This strong and consistent influence of December to February precipitation is illustrated in Fig. 5b for the chronology of all 25 studied birches (n = 69, r = 0.406, p < 0.01). Growth responses to summer temperature from June to August were negative (n = 75, r = −0.260, p < 0.05). From 1980 onwards growth responded negative to previous summer conditions (lag of one year between summer temperature and growth) (n = 35, r = −0.413, p < 0.05). In general, growth was negatively related to temperature
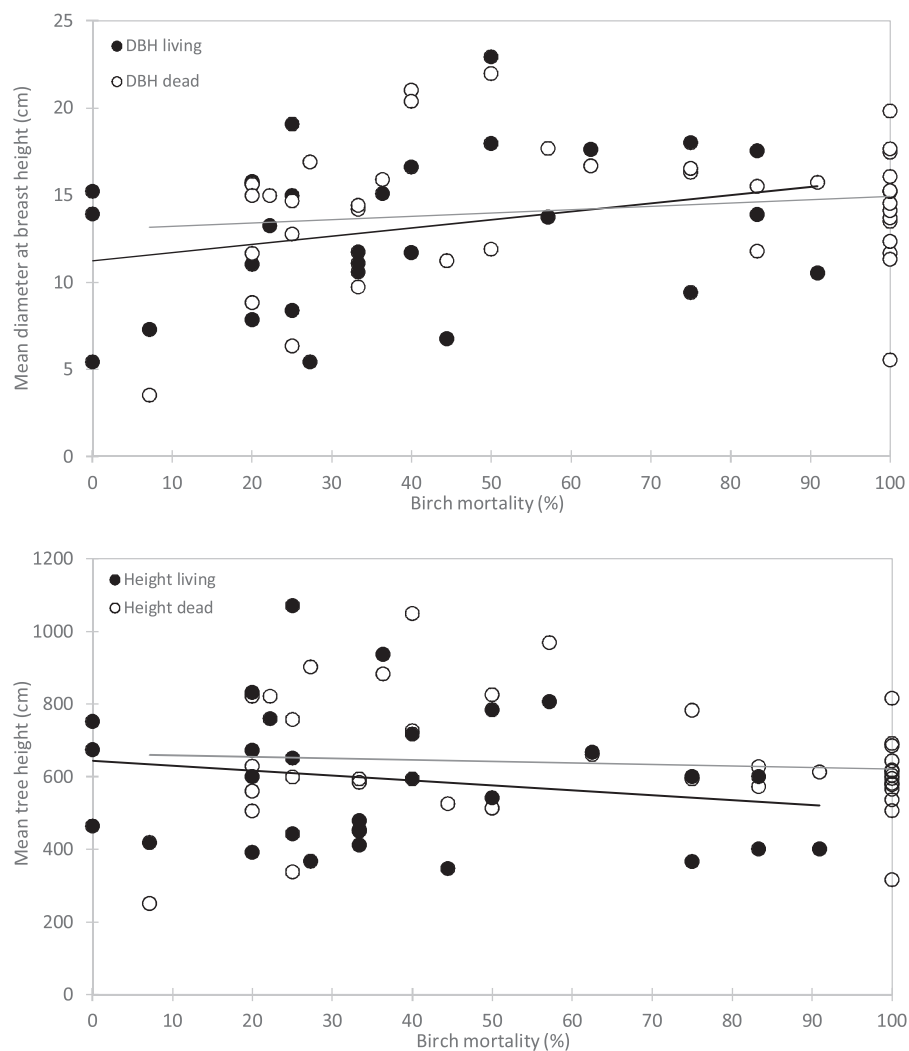

Fig. 3. Average birch tree mortality (%) in relation to (a) mean diameter at breast height of living (solid symbols, black line) and dead birch trees (open symbols, grey line), and (b) mean tree height of living (solid symbols, black line) and dead birch trees (open symbols, grey line) in the 44 plots.
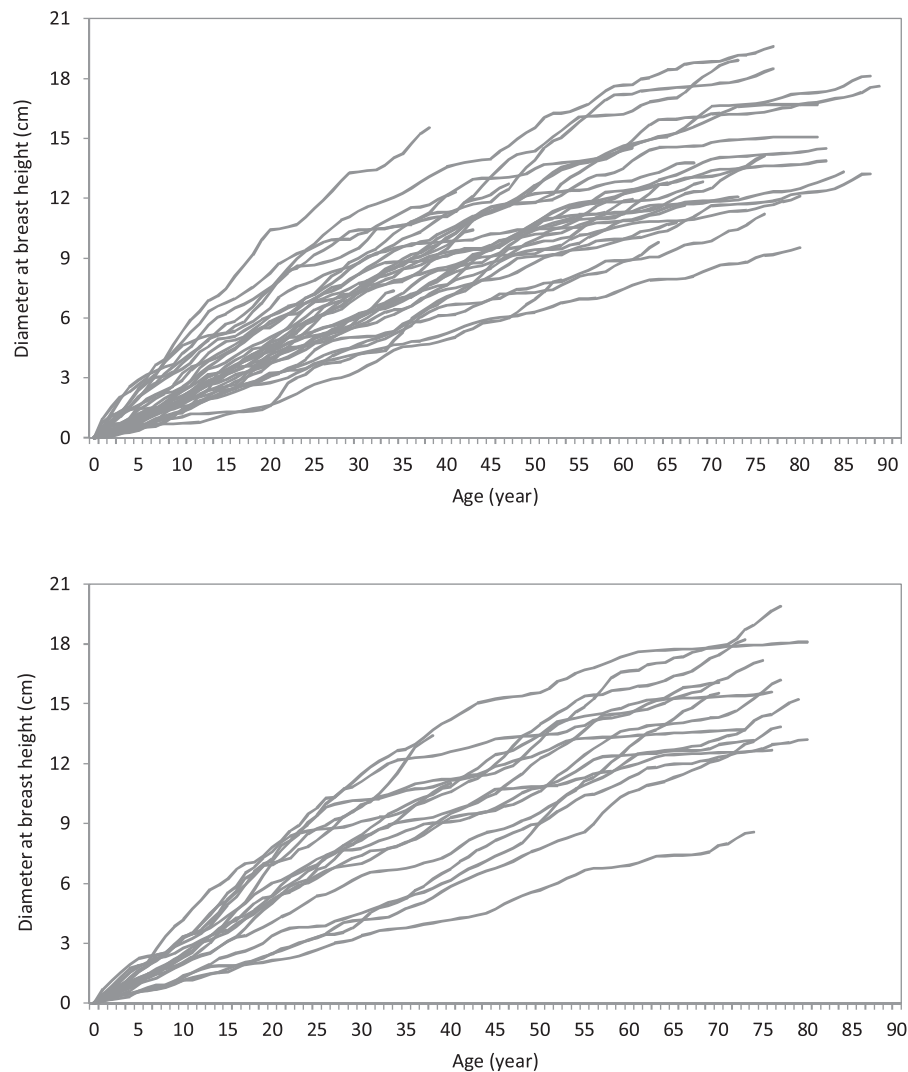
Fig. 4. Growth trajectories based on tree-ring width in either (a) the West forest (n = 32); or (b) the East forest (n = 17).

during the growing season (April to September) of the previous year (n = 74, r = −0.258, p < 0.05), which was stronger from 1980 onwards (n = 35, r = −0.480, p < 0.01).

4. Discussion

4.1. Tree mortality

Mortality of adult trees was higher in the West forest than in the East forest, as was deer density, but the relationship was not significant. This also holds for the frequency of bark stripping. A possible explanation is that density of dung pellet groups is an indirect and probably poor indicator of deer density, since it is only related to short-term deer density. It was, furthermore, suggested that birch seedlings face top-down control by red deer resulting in a lower frequency of the smaller DBH classes in forest areas where deer density is high. However, distribution of DBH classes was similar among the forest areas, indicating that a comparable factor is responsible for tree mortality in both areas. This supports our hypothesis that a climatic factor could be the main driver of tree mortality. Furthermore, in plots with mortality rates exceeding 50% fewer tall and small-diameter living trees were present. Tall trees (Bennett et al., 2015) and young/small-diameter trees are found to be more sensitive to climate-induced mortality (i.e. rising temperature and changes in precipitation patterns; Gradel et al., 2017).

Since the West forest is located at higher elevation (c. 1700 m), we assumed that the permafrost layer in this forest was closer to the soil surface than in the East forest (c. 1600 m), providing meltwater that contributes to soil moisture content (as measured in Mongolia by Zhang et al., 2006). However, tree mortality was highest and seed regeneration was almost absent in the West forest. The absence of seed regeneration could be explained by reduced forest cover due to mortality, leading to temperature extremes and increased evapotranspiration (Will et al., 2013) and hence reduced water availability. Regeneration, in particular in the West forest, occurred mainly from the root systems of adult trees, which is an alternative strategy when environmental conditions are poor and therefore could be taken as indicator for reduced water availability. A recent study by Gradel et al. (2017) reported that young birch trees are more sensitive to water availability than old birch trees (Gradel et al., 2017), which supports our suggestion that water availability is the most critical factor for seedling establishment. Browsing may increase the susceptibility of small-diameter trees to reduced water availability by weakening tree vigour (Pedersen, 1998).

4.2. Tree growth and climate

The similarity of tree growth depressions and releases in the chronologies of the West and East forest indicate that tree growth in both areas is influenced by the same external factor. Indeed,
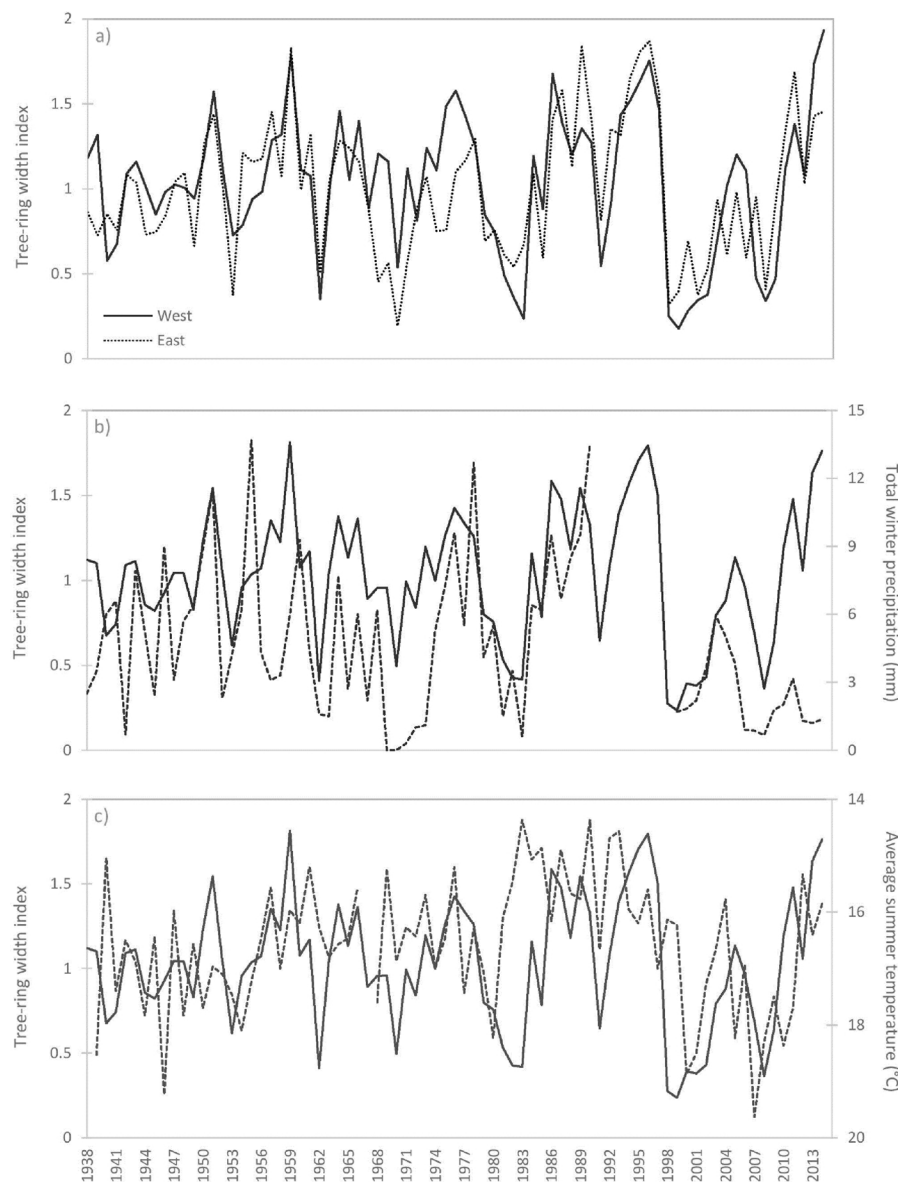
Fig. 5. Chronologies of (a) tree-ring width of the West forest (n = 16, solid line) and East forest (n = 9, dotted line); (b) mean chronology of both forests with winter precipitation (December–February; r = 0.406; dashed line, mm); and (c) mean chronology with average summer temperature (June–August; r = −0.260; dashed line, °C; temperature axis reversed).

precipitation was strongly correlated with tree growth in both areas. However, instead of the predicted positive effect of precipitation during the growing season, above-average winter (December–February) precipitation turned out to be most favourable for radial tree growth in both areas. The positive effect of precipitation is supported by other studies in the same region (winter precipitation: Gradel et al., 2017; mean annual precipitation: Anderegg et al., 2015; summer precipitation: Bao et al., 2015; Kharuk et al., 2013; Poulter et al., 2013) and expected to be related to the isolating capacity of the snow cover on the soil surface during winter (Bruland, 2002), that gradually melts during spring, contributing to the soil moisture content (Grippa et al., 2005). Additionally, average summer temperature had a negative, although less-strong, effect on tree growth in both areas. The negative correlation between birch growth and previous year's summer temperature is supported by another study in the same region (Gradel et al., 2017), reflecting a stronger dependence on water at the start of the growing season.

The strong effect of winter precipitation on annual tree growth indicates that winter precipitation is an essential factor in the forests of Hustai National Park, despite the fact that most rain falls during the growing season from April to September (Fig. 1c; Wallis de Vries et al., 1996). Winter precipitation is suggested to be a key factor in recharging the soil-water reserve for the following growing season (Neff and Wight, 1977; Gradel et al., 2017). Water availability is of crucial importance during the first part of the growing season as most of the annual growth ring is formed during this period (An et al., 2012). This is supported by the size of the most recent formed tree ring (extracted in July 2015), which was of average size in both forest areas, indicating that most growth occurs during the first months of the growing season.

The ring patterns furthermore indicated a growth recovery in the last decade. One explanation might be that recent growth recovery is related to reduced resource competition as a result of mortality of neighbouring trees. Additionally, the observed recent depressions in the ring patterns of less vital trees, which are stronger in the West forest than East forest, support the suggestion that trees that survive drought are more sensitive to subsequent drought events (Suarez et al., 2004), as recovery of their expected growth rate takes approximately 2–4 years (Anderegg et al., 2013). Furthermore, the strong variation in growth

rate between individual trees within each study area might be related to differences in microsite conditions (*e.g.* soil quality and soil moisture; Greenwood and Weisberg, 2008).

In conclusion, precipitation and temperature are found to be key factors determining tree growth in Hustai National Park. Winter precipitation through recharging the soil-water reserve provide optimal starting conditions, whereas high summer temperature can induce an earlier growth stop through increasing the evaporative demand. The predicted reduction of precipitation, especially during winter as observed in North China (Sui et al., 2013), due to global climate change (Sato et al., 2007), might cause a rapid conversion of the forest-steppe ecotone into a steppe ecosystem. The disappearance of the forest in Hustai National Park will strongly unbalance the interaction between red deer, wolf and Przewalski horse, threatening Mongolia's biodiversity.

Acknowledgements

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